

- studies: the staggered entry design. *Journal of Wildlife Management* 53:7–15.
- SAS INSTITUTE. 1996. SAS/STAT Software®: changes and enhancements through release 6.11. SAS Institute, Cary, North Carolina, USA.
- STRAW, J. A., JR., D. G. KREMENTZ, M. W. OLINDE, AND G. F. SEPIK. 1994. American woodcock. Pages 97–114 in T. C. Tacha and C. E. Braun, editors. *Migratory shore and upland game birds in North America*. International Association of Fish and Wildlife Agencies, Washington, D.C., USA.
- WHITING, R. M., JR., R. R. GEORGE, M. K. CAUSEY, AND T. R. ROBERTS. 1985. February hunting of American woodcock: breeding implications. Pages 309–317 in S. L. Beason and S. F. Roberson, editors. *Game harvest management*. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas, USA.
- WOOD, G. W., M. K. CAUSEY, AND R. M. WHITING, JR. 1985. Perspectives on American woodcock in the southern United States. *Proceedings of the North American Wildlife and Natural Resources Conference* 50:573–585.

Received 30 March 1999.

Accepted 12 April 2000.

Associate Editor: Bunck.

## DETERMINANTS OF LEAD SHOT, RICE, AND GRIT INGESTION IN DUCKS AND COOTS

RAFAEL MATEO, Laboratory of Toxicology, Faculty of Veterinary Medicine, Autonomous University of Barcelona, 08193 Bellaterra, Spain.

RAIMON GUITART, Laboratory of Toxicology, Faculty of Veterinary Medicine, Autonomous University of Barcelona, 08193 Bellaterra, Spain

ANDY J. GREEN, Department of Applied Biology, Estación Biológica de Doñana, CSIC, Avenida de María Luisa s/n, 41013 Sevilla, Spain

**Abstract:** We investigated the relationships between lead shot ingestion, grit size selection, bill morphology, and diet in a community of 8 duck species and common coot (*Fulica atra*) wintering in the Ebro Delta, Spain. There were no intraspecific differences related to sex or age in grit composition, lead shot, and rice-grain ingestion. Strong interspecific differences were recorded for all these variables and for the density of bill lamellae. The proportion of grit of size >1 mm (especially >2–3 mm) was positively correlated with the prevalence of lead shot ingestion, as well as with rice ingestion. Rice ingestion was also positively correlated with the prevalence of lead shot ingestion. Those duck species feeding on rice had larger grit and higher prevalences of lead shot than herbivorous species. Contrary to the predictions of a straining model for food or grit ingestion, lamellar density did not explain interspecific differences in grit selection, rice ingestion, or prevalence of lead shot ingestion. These findings contradict previous claims in the literature, and suggest that mechanisms other than straining are used by ducks for grit selection and lead shot ingestion.

*JOURNAL OF WILDLIFE MANAGEMENT* 64(4):939–947

**Key words:** Bill morphology, contamination, coot, duck, Ebro Delta, grain, grit, lamellae, lead shot, Spain.

Lead poisoning of Anatidae and other waterbirds, resulting from the ingestion of lead (Pb) shot discharged by hunters, is a conservation problem world-wide. It is particularly severe in coastal wetlands in Spain (Mateo et al. 1997, 1998) and other parts of the Mediterranean region (Pain 1990). However, the mechanisms underlying the ingestion of Pb shot remain unclear. Field and experimental studies suggest that Anatidae ingest Pb shot intentionally, confusing it with grit. Moore et al. (1998) observed similar prevalences of Pb shot ingestion in species of diving ducks with different foraging behaviors, and interpreted it as evidence that ducks actively selected shot as grit, as opposed

to ingesting shot accidentally with food. Many authors have observed relatively high prevalences of shot ingestion in species that consume grit of a size (2–3 mm in diameter) similar to shot (Hall and Fisher 1985, Pain 1990). Trost (1981) observed that captive mallards (*Anas platyrhynchos*) could differentiate between shot and grain mixed in a feeder, but this ability was less evident for shot and grit. Similar conclusions were obtained when offering grit, shot, and grain mixed with mud and water to mallards to mimic field conditions (Mateo and Guitart 2000).

However, the methods used by waterbirds to find and select grit are unclear. Some species,

such as greylag goose (*Anser anser*) and Eurasian wigeon (*Anas penelope*), can select grit visually (Sánchez et al. 1977, Thomas et al. 1977). Color, size, shape, and chemical composition of grit particles are used by many terrestrial bird species to select grit visually (Kopischke and Nelson 1966; Alonso 1985; Best and Gionfrido 1991, 1994; Gionfrido and Best 1996). Grit selection is likely to be less visual in many duck species owing to their dependency on flooded environments and their nocturnal activity patterns (McNeil et al. 1992). The duck bill and its maxillary lamellae constitute a sophisticated filtering apparatus (Zweers et al. 1977, Crome 1985, Kooloos et al. 1989). Several studies have found a negative relationship between the lamellar density and the size of invertebrates or seeds ingested by ducks (Thomas 1982, Nudds and Bowlby 1984, Nummi 1993), suggesting that the lamellae work like a filter to select food items. Interspecific differences in lamellar density are therefore thought to have considerable influence on the community ecology of the Anatidae (Nudds 1992). It has been suggested that the same mechanism functions in grit ingestion, with species that have higher lamellar densities selecting finer grit (Nudds 1992:552, Nudds and Wickett 1994:779).

We tested the value of this straining model in explaining differences among 9 waterbird species wintering in the Ebro Delta, Spain. We consider the interspecific relationships between lamellar densities, rates of ingestion of Pb shot or rice grain, and the selection of grit size. We also test for differences between sexes and age classes within species.

## STUDY AREA

Between 35,000 and 50,000 waterbirds are harvested using lead shot in the Ebro Delta every year (Martínez-Vilalta 1996). Assuming that 3–5 cartridges with 300 shot pellets/cartridge are used per harvested bird, the annual input in the area can be estimated at 31.5–75.0 million Pb shot. The Ebro Delta covers 350 km<sup>2</sup> and hunting is allowed in 276 km<sup>2</sup> but concentrated mainly in lagoons and rice fields with a total area of 52 km<sup>2</sup>. Thus an estimated 0.6–1.4 shot/m<sup>2</sup> are deposited every year in these parts of the Ebro Delta. Studies of the top 20 cm of sediment from 7 hunting areas in 1991–96 revealed densities of 6–83 shot/m<sup>2</sup> in the rice fields and 97–266 shot/m<sup>2</sup> in the lagoons (Guitart et al. 1994, Mateo et al. 1997, Mateo 1999).

Rice grains are a major food of waterbirds wintering in the area (Llorente 1984). The area flooded or under cultivation and the proportion of waterfowl affected by Pb shot ingestion did not vary between years during the study (Mateo 1999).

## METHODS

A total of 379 birds from 8 duck species plus common coot were taken from the bags of hunters during the 1991–96 hunting seasons (Guitart et al. 1994, Mateo et al. 1997, Mateo 1999). Sex was determined by examination of the gonads and age (1st yr or adult) was determined by the presence of Fabricius Bursae (Heitmeyer et al. 1993). Wing plumage characteristics were also used for sexing and ageing following Boyd et al. (1975).

Gizzards were examined externally for the presence of shot entry holes to establish whether any shot found within had been shot-in or ingested. Each gizzard was cut with scissors and its content washed with water and then dried. Vegetation was removed by flotation in chloroform. The precipitate was dried and placed in plastic Petri dishes. After Pb shot were removed, grit was sieved (sieve sizes: 4, 3, 2, 1.5, 1, and 0.5 mm) and each size class of particles was weighed (Guitart et al. 1994). The presence or absence of rice grains (with a typical size of 2.2 × 3.3 × 8.6 mm) was noted.

With the following exceptions, lamellar density was studied in 6 males and 6 females from each of the duck species. Only 4 female gadwall (*Anas strepera*), 5 female Eurasian wigeon, 5 male common teal (*A. crecca*), and 3 female red-crested pochard (*Netta rufina*) were available. Using methods similar to those of Kehoe and Thomas (1987), lamellar density (lamellae/cm) in the upper mandible was obtained by measuring the distance between the first 20 lamellae to the front of the nostril. A needle was pushed through to the outer side of the first and twentieth lamellae, and the distance between them was measured.

Differences between sexes and ages in the total weight of gizzard grit within the 2 species with large sample sizes, mallard and northern pintail (*A. acuta*), were tested with an ANOVA. Interspecific differences between the total weights of grit and lamellar densities were tested with 1-way-ANOVAs, using a Tukey test to establish post-hoc differences between species. Because of the unit-sum constraint of grit size

Table 1. Lamellar density (lamellae/cm) and percentage of occurrence of Pb shot pellets and rice in gizzards in waterbirds wintering in the Ebro Delta, Spain, 1991–96. Gizzards with no food material were excluded when considering the percent occurrence of rice.

Species	Lamellar density <sup>a</sup>			Occurrence <sup>b</sup>			
	n	$\bar{x}$	SE	Pb shot		Rice	
				n	%	n	%
Eurasian wigeon	11	9.91 <sup>CD</sup>	0.23	25	4.0 <sup>DE</sup>	25	36.0 <sup>DF</sup>
Gadwall	10	10.48 <sup>D</sup>	0.16	25	8.0 <sup>CDE</sup>	15	13.3 <sup>EF</sup>
Common Teal	11	13.29 <sup>E</sup>	0.26	35	22.9 <sup>BCD</sup>	27	66.7 <sup>BCD</sup>
Mallard	12	7.70 <sup>B</sup>	0.14	86	30.2 <sup>B</sup>	80	76.3 <sup>BC</sup>
Northern pintail	12	9.33 <sup>C</sup>	0.15	97	74.2 <sup>A</sup>	90	81.1 <sup>AB</sup>
Northern shoveler	12	19.89 <sup>F</sup>	0.38	36	27.8 <sup>BC</sup>	19	68.4 <sup>BD</sup>
Red-crested pochard	9	6.09 <sup>A</sup>	0.12	21	19.0 <sup>BCDE</sup>	16	50.0 <sup>CDE</sup>
Common pochard	12	9.08 <sup>C</sup>	0.14	26	69.2 <sup>A</sup>	23	95.7 <sup>A</sup>
Common coot				28	3.6 <sup>E</sup>	28	0.0 <sup>F</sup>

<sup>a</sup> Two values in the same column with the same capital letter did not differ in Tukey tests,  $P > 0.05$ .

<sup>b</sup> Two values in the same column with the same capital letter did not differ in  $\chi^2$  tests,  $P > 0.05$ .

fractions for each individual duck, differences in grit composition due to sex and age (for mallard and northern pintail) or among species were studied by means of a compositional analysis of the fractions as percentages (Aitchison 1986), using a MANOVA of the log ratios of each fraction (divided by grit  $\leq 0.5$  mm).

The prevalence of Pb shot ingestion and the presence of rice in the gizzard were compared by sex and age (for mallard and pintail) or between species with a  $\chi^2$  test (Yates's corrected) or a Fisher's exact probability test (the latter when an expected cell value was  $< 5$ ). Interspecific relationships between lamellar density, total weight of grit, proportion of each fraction of grit, prevalence of Pb shot ingestion and rice ingestion (% occurrence) were studied with Pearson's correlations between the mean values for each species. Within mallard and pintail, the weight and proportion of grit  $> 2$ mm (similar in size to Pb shot), were compared for birds with and without ingested shot using a Student  $t$ -test.

## RESULTS

### Lamellar Density

Strong interspecific differences in lamellar densities were observed ( $F_{7,81} = 290.7$ ,  $P < 0.001$ ), although the differences between common pochard (*Aythya ferina*), northern pintail, and Eurasian wigeon were not significant (Table 1). Likewise, the difference between wigeon and gadwall was not significant (Table 1).

### Grit Selection

No significant differences between sexes or ages in the total weight of grit or its size composition were detected in mallard or northern pintail (all with  $P > 0.1$ , Table 2).

Significant interspecific differences were observed for both total weight of grit ( $F_{8,370} = 122.6$ ,  $P < 0.0001$ ) and for their size compositions (Wilks's  $\lambda = 0.2$ ,  $P = 0.0001$ ). The order of the total weight of grit was as follows: common coot  $>$  red-crested pochard  $\geq$  gadwall  $>$

Table 2. Percentage of occurrence of Pb shot pellets and rice, and total weight of grit in gizzards of mallards and northern pintails wintering in the Ebro Delta, Spain, 1991–96. Gizzards with no food material were excluded when considering the percentage of occurrence of rice.

Species	Sex or age	Occurrence				Total grit (g)		
		Pb shot		Rice		n	$\bar{x}$	SE
		n	%	n	%			
Mallard	M	42	30.9	38	84.2	42	1.01	0.12
	F	44	29.5	42	69.0	44	0.87	0.14
	J	34	29.4	32	78.1	34	1.01	0.16
	A	39	35.9	35	74.3	39	1.01	0.15
Northern pintail	M	54	74.1	48	83.3	54	1.37	0.13
	F	43	74.4	42	78.6	43	1.27	0.12
	J	40	75.0	40	82.5	40	1.11	0.11
	A	47	72.3	40	77.5	47	1.43	0.14

Eurasian wigeon > common pochard  $\geq$  northern pintail  $\geq$  northern shoveler (*A. clypeata*)  $\geq$  mallard  $\geq$  common teal (Fig. 1). As for the composition of grit size, 2 species groups were observed (Fig. 1): species with grit mainly >1 mm (common pochard, northern pintail, mallard, and northern shoveler) and species with grit predominantly  $\leq$ 1 mm (gadwall, Eurasian wigeon, common coot, red-crested pochard, and common teal). Tests comparing species pairs using compositional analysis of percent fractions were all significant ( $P < 0.03$ ) except for common coot vs. red-crested pochard and northern shoveler vs. mallard.

### Lead Shot and Rice Ingestion

No intraspecific differences between age categories or sexes were detected in the prevalence of lead shot or the frequency of rice ingestion in mallard or northern pintail (all with  $P > 0.18$ , Table 2). There were strong interspecific differences in prevalence of Pb shot (Table 1), which allowed the species to be divided into the following 3 groups. The highest prevalences were observed in northern pintail and common pochard; intermediate values were found in mallard, northern shoveler, common teal, and red-crested pochard; and the lowest values were found in gadwall, Eurasian wigeon, and common coot.

Interspecific differences in rice ingestion were similar to those for Pb shot prevalences (Table 1). The highest frequencies of rice occurrence in gizzards were in common pochard and northern pintail. Mallard, northern shoveler, common teal, and red-crested pochard were intermediate, and the lowest frequencies were in Eurasian wigeon, gadwall, and common coot.

### Relationship between Lamellar Density, Grit Selection, and Shot and Rice Ingestion

Among species, Pb shot ingestion was positively correlated with the selection of grit fractions >1 mm (Table 3), especially those >3–4 mm in diameter (Fig. 2). However, this trend was not observed intraspecifically, because mallards and northern pintails with ingested shot did not have a greater weight or proportion of grit >2 mm than those without. On the contrary, mallards with ingested shot had less grit >2 mm ( $n = 26$ ,  $\bar{x} \pm \text{SE}$ ;  $0.07 \pm 0.01$  g) than those without ( $n = 60$ ,  $0.18 \pm 0.05$  g;  $t_{67.9} = 2.01$ ,  $P = 0.049$ ). The presence of rice grains in

the gizzard of species was positively correlated with the frequency of grit of >1–4 mm, and negatively with grit  $\leq 0.5$  mm and total grit (Table 3). Lamellar density was not significantly correlated with grit selection, Pb shot prevalence, or rice ingestion, but the occurrence of Pb shot ingestion was positively correlated with the occurrence of rice ingestion ( $r = 0.823$ ,  $P < 0.01$ ).

### DISCUSSION

Ducks and coots have various strategies for feeding (Thomas 1982, Pöysä 1983) and these strategies can potentially be used for ingesting grit. In aquatic media, ducks can feed by filtration using the tongue and bill as a suction-pressure pump. This process generates a flow of water with particles into the mouth, which are then forced laterally through the middle and rear parts of the gape. The particles are trapped and brushed by the maxillary lamellae and the tongue to the back of the mouth, where they are swallowed (Zweers et al. 1977, Kooloos et al. 1989). A simple straining process would therefore allow species with higher lamellae densities to filter smaller items (Nudds and Bowlby 1984). Laboratory research shows that, while lamellae act as a sieve to some extent, the bill and tongue work in a sophisticated manner (e.g. via centrifugation) that allows ducks to filter out finer particles than would be possible with a simple sieving process (Crome 1985, Kooloos et al. 1989).

Our results show that the straining model cannot explain interspecific differences in grit selection, and suggest that grit is not generally ingested via sieving with the lamellae in this manner. We found no interspecific relationship between lamellar density and grit size, and in some species the most abundant grit sizes were smaller than their interlamellar distances (Fig. 1). Both ducks and coots seem likely to select most grit using other methods such as grubbing into the substrate and surface picking (Thomas 1982). Although Nudds (1992) and Nudds and Wickett (1994) suggested that lamellar density explains interspecific differences in grit size, this is not the case either in our study or when reassessing previous work. In Europe, grit size data from various duck species in England (Thomas et al. 1977) and France (Pain 1990) show no relationship with published data on lamellar density (Table 3; Thomas 1982, Nudds et al. 1994). The same is true in Australia,

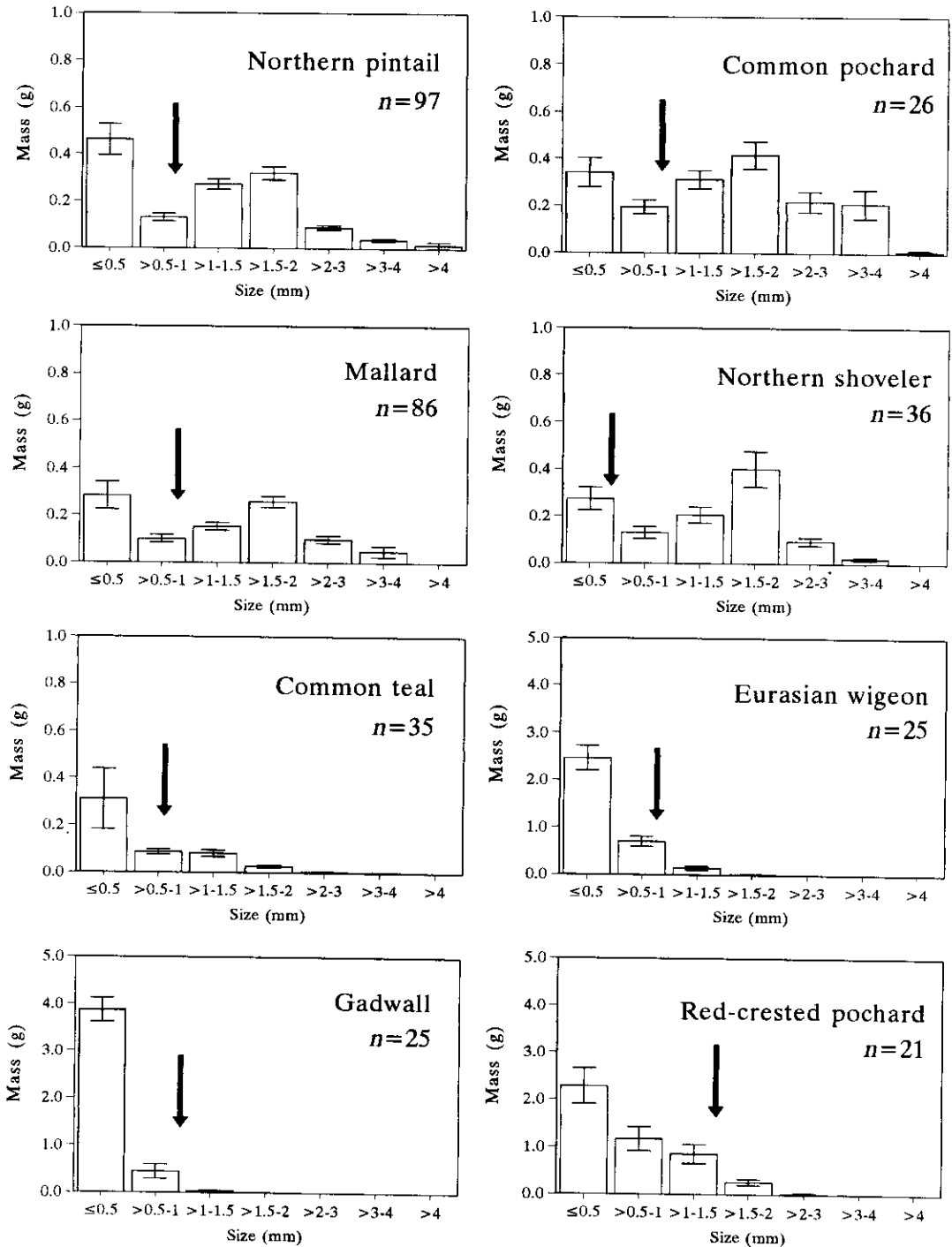


Fig. 1. Mass ( $\bar{x} \pm S.E.$ ) of the different grit size categories obtained from the gizzards of 8 duck species wintering in the Ebro Delta, Spain, 1991–96. The mean width of the interlamellar gap of each species is marked with an arrow.

Table 3. Pearson's correlation coefficients for the different grit size categories (% mass) with the lamellar density (lamellae/cm) and the occurrence (%) of Pb shot and rice in gizzards of 9 species of waterbirds wintering in the Ebro Delta, Spain, 1991–96 (coot was excluded from correlations involving lamellar density).

Grit size categories	Lamellar density	Occurrence	
		Pb shot	Rice
≤ 0.5 mm	0.081 <sup>ns</sup>	-0.737*	-0.854***
>0.5–1 mm	0.105 <sup>ns</sup>	-0.579 <sup>ns</sup>	-0.428 <sup>ns</sup>
>1–1.5 mm	-0.017 <sup>ns</sup>	0.676*	0.788*
>1.5–2 mm	-0.188 <sup>ns</sup>	0.665 <sup>ns</sup>	0.758*
>2–3 mm	-0.023 <sup>ns</sup>	0.770*	0.789*
>3–4 mm	0.072 <sup>ns</sup>	0.828**	0.699*
>4 mm	0.053 <sup>ns</sup>	0.727*	0.308 <sup>ns</sup>
Total grit	0.493 <sup>ns</sup>	-0.587 <sup>ns</sup>	-0.861***

<sup>ns</sup>not significant ( $P > 0.05$ ), \* $P \leq 0.05$ , \*\* $P \leq 0.01$ , \*\*\* $P \leq 0.005$ .

where of 4 duck species studied by Crome (1985), the grey teal (*A. gibberifrons*) had the lowest lamellar density (i.e. the highest interlamellar distance) yet consumed the smallest grit (Norman and Brown 1985). In some previous studies, larger bodied species tended to have larger grit, consume larger prey, and have lower lamellar densities (Weller 1972, Livezey 1989). However, it is body size rather than lamellar density that seems to underlie such relationships.

It is not surprising that the simple straining model does not explain differences between duck species in the ingestion of Pb shot and rice grains, since both items are much larger than the interlamellar gaps in any species (i.e. both items could be filtered out by all species). Clearly, there are limitations of the straining model in explaining dietary differences between duck species. Although several studies have found that ducks with higher lamellar densities feed on smaller items (Thomas 1982, Nudds and Bowlby 1984, Nummi 1993), this is far from a universal pattern. Ducks have flexible feeding strategies and species capable of feeding on small items may ignore them to concentrate on larger ones when these are abundant, e.g. as in the consumption of rice by northern shoveler and common teal in this study. Similarly, Batzer et al. (1993) found mallards to select amphipods >5 mm in length, much larger than their interlamellar gap.

We have not studied sexual differences in lamellar density because of the small sample size, but previous studies with larger sample sizes have shown males to have a lower density in many duck species (Nudds and Kaminski 1984,

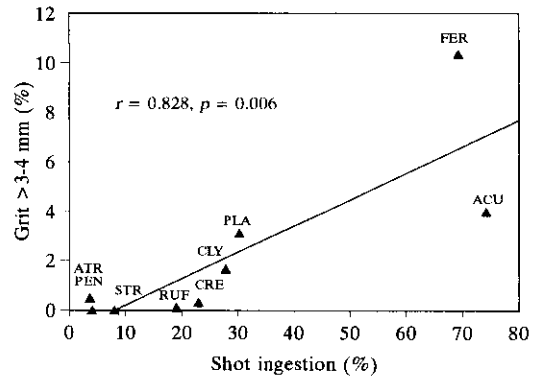


Fig. 2. Relationship between abundance of grit fraction of 3–4 mm (% of the total grit weight) and the prevalence of Pb shot ingestion in 9 waterfowl species wintering in the Ebro Delta, Spain, 1991–96 (ATR: common coot, PEN: Eurasian wigeon, STR: gadwall, RUF: red-crested pochard, CRE: common teal, CLY: northern shoveler, PLA: mallard, ACU: northern pintail, and FER: common pochard).

Livezey 1989), including mallard and northern pintail. However, such differences were not reflected in sexual differences in grit selection or Pb exposure in either species in our study.

Differences in Pb exposure due to sex or age in waterbird populations have been observed by several authors (Hoffmann 1960, Hohman et al. 1990, Merchant et al. 1991, DeStefano et al. 1992, Samuel et al. 1992), but others have found no such differences (Mudge 1983, Pain 1990, Havera et al. 1992, current study). Differences in grit selection can translate into different Pb exposures, but we have found no such differences in mallard and northern pintail. Other studies have found more grit in male mallard, Eurasian wigeon, gadwall, and purple swamphen (*Porphyrio porphyrio*), than females (Thomas et al. 1977, Norman and Mumford 1985, Pain 1990). Moreover, Trost (1981) found a higher experimental consumption of grit by male mallards during the fall and winter, whereas females consumed more grit in spring and summer.

Our study provides further evidence that Pb shot are mainly ingested by waterbirds because they are confused with grit, and that differences between species in exposure to Pb are related to differences in grit selection, which in turn are explained by interspecific differences in diet. Species with high occurrence of rice in their gizzards (common pochard, northern pintail, mallard, and northern shoveler) had larger grit (especially sizes >1 mm) and were most exposed to Pb shot. In contrast, those taking less

rice (gadwall, Eurasian wigeon, and common coot) had finer grit and lower Pb prevalence. Larger grit is effective for breaking seeds, whereas smaller sand particles are used to cut and grind leaves (Thomas et al. 1977). Furthermore, herbivorous ducks have a relatively large gizzard and more grit because they must process large amounts of green plant material, which is less rich in energy than seeds (Barnes and Thomas 1986).

The relationship between Pb exposure and selection of grit particles similar in size to shot has been established by Pain (1990), who described a correlation between the prevalence of Pb shot and the mean weight of grit >2 mm in 7 duck species in the Camargue, France. This suggests that most Pb shot are ingested when birds are seeking grit and agrees with the experimental observations of Trost (1981) and Mateo and Guitart (2000) in captive mallards. However, since the presence of grit >2 mm is also well correlated with the ingestion of large seeds, such as rice, we can not rule out the possibility that some Pb shot are mistakenly ingested for seeds (Whitehead and Tschirner 1991). Indeed, grit ingestion and feeding on seeds may sometimes occur simultaneously and some overlap in mechanism is probably inevitable. Furthermore, we failed to find any intraspecific relationships between grit size and Pb shot prevalence as may be expected if Pb shot were confused for grit. The absence of such a relationship may be because intraspecific variation in grit size does not reflect different individual preferences but rather variation in encounter rates with different grit sizes.

We suggest that grubbing or surface picking (Thomas 1982) are the main mechanisms for grit and Pb shot ingestion, although some role for straining in some species can not be ruled out on the basis of our observations. Further studies with ducks in captivity are needed to clarify the mechanisms of shot and grit ingestion.

## MANAGEMENT IMPLICATIONS

Many authors have recommended grit supplementation to alleviate Pb poisoning (Trost 1981, Pain 1990, Moore et al. 1998). However, little is known about the methods used by waterbirds to ingest grit. In this study, we found no relationship between the density of maxillary lamellae (structures that retain food particles by straining) and grit composition or the preva-

lence of Pb shot. This suggests that waterfowl take most grit independently of feeding activity, which is important for the development of grit supplementation as a measure to reduce lead poisoning. However, more research on grit selection, including where and how waterbirds take grit, is essential if such measures are to be developed successfully.

## ACKNOWLEDGMENTS

This work was supported by the Wildlife Service of the Spanish Ministry of Environment, Fisheries and Food, and by the Department of Agriculture, Livestock, and Fisheries of the Autonomous Government of Catalonia. The authors are grateful to the hunters and personnel of the Ebro Delta Natural Park (especially A. Martínez-Vilalta) for their field assistance in collecting birds for this study. We also thank P. Puig for his statistical advice.

## LITERATURE CITED

- AITCHISON, J. 1986. The statistical analysis of compositional data. Chapman & Hall, London, United Kingdom.
- ALONSO, J. C. 1985. Grit in the gizzard of Spanish sparrows (*Passer hispaniolensis*). *Die Vogelwarte* 33:135-143.
- BARNES, G. G., AND V. G. THOMAS. 1986. Digestive organ morphology, diet and guild structure of North American Anatidae. *Canadian Journal of Zoology* 65:1812-1817.
- BATZER, D. P., M. MCGEE, AND V. H. RESH. 1993. Characteristics of invertebrates consumed by mallards and prey response to wetland flooding schedules. *Wetlands* 13:41-49.
- BEST, L. B., AND J. P. GIONFRIDO. 1991. Characterization of grit use by cornfield birds. *Wilson Bulletin* 103:68-82.
- , AND ———. 1994. Effects of surface texture and shape on grit selection by house sparrows and northern bobwhite. *Wilson Bulletin* 106:689-695.
- BOYD, H., J. G. HARRISON, AND A. ALLISON. 1975. Duck wings—A study of duck production. WAGBI, Rossett, United Kingdom.
- CROME, F. H. J. 1985. An experimental investigation of filter-feeding on zooplankton by some specialized waterfowl. *Australian Journal of Zoology* 33: 849-862.
- DESTEFANO, S., C. J. BRAND, AND D. H. RUSCH. 1992. Prevalence of lead exposure among age and sex cohorts of Canada geese. *Canadian Journal of Zoology* 70:901-906.
- GIONFRIDO, J. P., AND L. B. BEST. 1996. Grit color selection by house sparrows and northern bobwhites. *Journal of Wildlife Management* 60:836-842.
- GUITART, R., J. TO-FIGUERAS, R. MATEO, A. BERTOLERO, S. CERRADELO, AND A. MARTÍNEZ-VILALTA. 1994. Lead poisoning in waterfowl from the Ebro Delta, Spain: Calculation of lead expo-

- sure thresholds for mallards. *Archives of Environmental Contamination and Toxicology* 27: 289–293.
- HALL, S. L., AND F. M. JR FISHER. 1985. Lead concentrations in tissues of marsh birds: Relationship of feeding habits and grit preference to spent shot ingestion. *Bulletin of Environmental Contamination and Toxicology* 35:1–8.
- HAVERA, S. P., R. M. WHITTON, AND R. T. SHEALY. 1992. Blood lead and ingested and embedded shot in diving ducks during spring. *Journal of Wildlife Management* 56:539–545.
- HEITMEYER, M. E., L. H. FREDRICKSON, AND D. D. HUMBURG. 1993. Further evidence of biases associated with hunter-killed mallards. *Journal of Wildlife Management* 57:733–740.
- HOFFMANN, L. 1960. Le saturnisme fleau de la sauvagine en Camargue. *Terre et Vie* 107:120–131.
- HOHMAN, W. L., R. D. PRITCHERT, R. M. PACE III, D. W. WOOLINGTON, AND R. HELM. 1990. Influence of ingested lead on body mass of wintering canvasbacks. *Journal of Wildlife Management* 54: 211–215.
- KEHOE, F. P., AND V. G. THOMAS. 1987. A comparison of interspecific differences in the morphology of external and internal feeding apparatus among North American Anatidae. *Canadian Journal of Zoology* 65:1818–1822.
- KOOLOOS, J. G. M., A. R. KRAAIJEVELD, G. E. J. LANGENBACH, AND G. A. ZWEERS. 1989. Comparative mechanics of filter feeding in *Anas platyrhynchos*, *Anas clypeata* and *Aythya fuligula* (Aves, Anseriformes). *Zoomorphology* 108:269–290.
- KOPISCHKE, E. D., AND M. M. NELSON. 1966. Grit availability and pheasant densities in Minnesota and South Dakota. *Journal of Wildlife Management* 30:269–275.
- LIVEZEY, B. C. 1989. Feeding morphology, foraging behavior, and foods of steamer ducks (Anatidae: *Tachyeres*). Occasional Papers of the Museum of Natural History 126:1–41. The University of Kansas, Lawrence, Kansas, USA.
- LLORENTE, G. 1984. Contribución al conocimiento de la biología y la ecología de cuatro especies de anátidas en el Delta del Ebro. Dissertation, Universitat de Barcelona, Barcelona, Spain.
- MARTÍNEZ-VILALTA, A. 1996. Gestión cinegética de las aves acuáticas: El caso del Delta del Ebro. In *Resúmenes de las XIII Jornadas Ornitológicas Españolas*, Figueras 1996. Sociedad Española de Ornitología, Madrid, Spain.
- MATEO, R. 1999. La intoxicación por ingestión de perdigones de plomo en aves silvestres: aspectos epidemiológicos y propuestas para su prevención en España. Dissertation, Universitat Autònoma de Barcelona, Bellaterra, Spain.
- , J. BELLURE, J. C. DOLZ, J. M. AGUILAR SERRANO, AND R. GUITART. 1998. High prevalences of lead poisoning in wintering waterfowl in Spain. *Archives of Environmental Contamination and Toxicology* 35:342–347.
- , AND R. GUITART. 2000. The effects of grit supplementation and feed type on steel-shot ingestion in mallards. *Preventive Veterinary Medicine* 44:221–229.
- , A. MARTÍNEZ-VILALTA, AND R. GUITART. 1997. Lead shot pellets in the Ebro Delta, Spain: Densities in sediments and prevalences of exposure in waterfowl. *Environmental Pollution* 96: 335–341.
- MCNEIL, R., P. DRAPEAU, AND J. D. GOSS-CUSTARD. 1992. The occurrence and adaptive significance of nocturnal habits in waterfowl. *Biological Reviews* 67:381–419.
- MERCHANT, M. E., S. S. SHUKLA, AND H. A. AKERS. 1991. Lead concentrations in wing bones of the mottled duck. *Environmental Toxicology and Chemistry* 10:1503–1507.
- MOORE, J. L., W. L. HOHMAN, T. M. STARK, AND G. A. WEISBRICH. 1998. Shot prevalences and diets of diving ducks five years after the ban on use of lead shotshells at Catahoula Lake, Louisiana. *Journal of Wildlife Management* 62:564–569.
- MUDGE, G. P. 1983. The incidence and significance of ingested lead pellet poisoning in British wildfowl. *Biological Conservation* 27:333–372.
- NORMAN, F. I., AND R. S. BROWN. 1985. Gizzard grit in some Australian waterfowl. *Wildfowl* 36:77–80.
- , AND L. MUMFORD. 1985. Studies on the purple swamphen, *Porphyrio porphyrio*, in Victoria. *Australian Wildlife Research* 12:263–278.
- NUDDS, T. D. 1992. Patterns in breeding waterfowl communities. Pages 540–567 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec and G. L. Krapu, editors. *Ecology and Management of Breeding Waterfowl*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- , AND J. N. BOWLBY. 1984. Predator-prey size relationships in North American dabbling ducks. *Canadian Journal of Zoology* 62:2002–2008.
- , AND R. M. KAMISKI. 1984. Sexual size dimorphism in relation to resource partitioning in North American dabbling ducks. *Canadian Journal of Zoology* 62:2009–2102.
- , K. SJÖBERG, AND P. LUNDBERG. 1994. Ecological relationships between Palearctic dabbling ducks on Baltic coastal wetlands and a comparison with the Nearctic. *Oikos* 69:295–303.
- , AND R. G. WICKETT. 1994. Body size and seasonal coexistence of North American dabbling ducks. *Canadian Journal of Zoology* 72:779–782.
- NUMMI, P. 1993. Food-niche relationships of sympatric mallard and green-winged teal. *Canadian Journal of Zoology* 71:49–55.
- PAIN, D. J. 1990. Lead shot ingestion by waterbirds in the Camargue, France: An investigation of levels and interspecific differences. *Environmental Pollution* 66:273–285.
- PÖYSÄ, H. 1983. Resource utilization pattern and guild structure in a waterfowl community. *Oikos* 40:295–307.
- SAMUEL, M. D., E. F. BOWERS, AND J. C. FRANSON. 1992. Lead exposure and recovery rates of black ducks banded in Tennessee. *Journal of Wildlife Diseases* 28:555–561.
- SÁNCHEZ, A., J. CASTROVIEJO, AND M. DELIBES. 1977. On the wintering of greylag geese in the Marismas of the Guadalquivir (Southwestern Spain). *Proceedings of the International Congress of Game Biologists* 13:65–76.
- THOMAS, G. J. 1982. Autumn and winter feeding ecol-



- ogy of waterfowl at the Ouse Washes, England. *Journal of Zoology*, London 197:131-172.
- , M. OWEN, AND P. RICHARDS. 1977. Grit in waterfowl at the Ouse Washes, England. *Wildfowl* 28:136-138.
- TROST, R. E. 1981. Dynamics of grit selection and retention in captive mallards. *Journal of Wildlife Management* 45:64-73.
- WELLER, M. W. 1972. Ecological studies of Falkland Islands' waterfowl. *Wildfowl* 23:25-44.
- WHITEHEAD, P. J., AND K. TSCHIRNER. 1991. Lead shot ingestion and lead poisoning of magpie geese *Anseranas semipalmata* foraging in a Northern Australian hunting reserve. *Biological Conservation* 58:99-118.
- ZWEERS, G. A., A. F. C. GERRITSEN, AND P. J. VAN KRANENBURG-VOOGD. 1977. Mechanics of feeding of the mallard (*Anas platyrhynchos* L.; Aves, Anseriformes). Basel, New York, USA.

Received 15 December 1999.

Accepted 12 May 2000.

Associate Editor: Rattner.